

CONTRIBUTION TO THE TAXONOMY AND PHYLOGENY
OF THE GENUS *POLIA* OCHSENHEIMER, 1816
(NOCTUIDAE, NOCTUINAE, HADENINI): SPECIES GROUPS AND
PAIRS IN THE HOLARCTIC SUBGENUS *POLIA* S. STR.

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We review the phylogenetic and biogeographical connections of the Holarctic subgenus *Polia*, re-considering the diagnoses of the species groups based on the external morphology and the characterisation of the male and female genitalia, as well. We produced trees based on genital morphological characters. A preliminary CO1 consensus tree was also constructed which generally supports the morphologically outlined species groups. The plesiomorphic abdominal brush organ was observed to become lost in different species groups independently. The asymmetrisation of the tufts of bristles on the saccular extensions represents one of the most important traits of the genus. These are weakly differentiated, and the shape is nearly symmetrical in supposedly plesiomorphic character states. The most differentiated asymmetrical saccular processes were found in *P. serratilinea* and, parallel, also in the species of the Holarctic *P. nebulosa* group. Holarctic connections are present in most Arctic-Boreal species and certain sister species and/or species groups in temperate taxa (i.e. in the *P. bombycina* and the *P. nebulosa* species groups), with subsequent speciation in the Nearctic. It means that Trans-Beringian migrations should have occurred at least three times in the geographical history of *Polia*, from which the trans-migration of the basally split *P. nebulosa* group was the most ancient.

Key words: diagnosis, consensus tree, genital morphology, character status, sister species, biogeography, *Polia*, Noctuidae.

INTRODUCTION

Preliminary considerations on phylogeny and biogeography

In a recent review paper (VARGA *et al.* 2017) we considered the taxonomic subdivision of the genus *Polia*, providing an annotated checklist of the Palearctic species, the descriptions of three new subgenera, and the re-definition of the nominotypical subgenus *Polia* s.str. This latter subgenus has, however, a Holarctic distribution; therefore we intend to consider here the phylogenetic and biogeographical connections of the entire group. The importance of Trans-Holarctic connections in the formation of the Noctuidae fauna of arctic

and boreal Eurasia and North America was discussed in detail at the end of the last century (e.g. LAFONTAINE & WOOD 1988, LAFONTAINE & KONONENKO 1988, KONONENKO *et al.* 1989, 1996, LAFONTAINE *et al.* 1983, 1987, 1991, MIKKOLA *et al.* 1991). The existence of such connections was already revealed, however, in the earlier survey of HEYDEMANN (1944) on the so-called “*Dualspezies*” of the genus *Polia* (syn.: *Aplecta* Guenée, 1850). Heydemann provided a detailed diagnosis of the genus, including the external morphology and the characterisation of the male and female genitalia, as well. The diagnosis of the genus, together with certain allied genera (*‘Polia complex’*) was reviewed by McCABE (1980), summarising in keys the external and genitalia characters.

From the diagnosis of the male genitalia, we have to exhibit the following characters. Dorsal arm of valvae is strongly sclerotised with well-developed cucullus, bearing some bristles of corona and a single (or exceptionally two) angular thorn(s); clavus is fused with the dilated baso-dorsal margin of the sacculus; saccular processes are moderately or strongly elongate, usually with more or less asymmetrical tufts of strong and long, fixed bristles; harpe is most often reduced to its basal plate, only a few exceptions are known; ampulla is, like a clasper, usually present; juxta is medio-dorsally more sclerotised and extended; aedeagus elongate, regularly with bill-shaped ventral carinal sclerotisation; vesica tubular, coiled or retroflexed (in one case helicoidal), with a subbasal and most often also with a medial diverticulum and a variably long distal field of fasciculate cornuti.

In the female genitalia, antrum is broad, sclerotised, often funnel-shaped; ductus bursae is elongate and flattened, moderately or strongly sclerotised; corpus bursae is ample, saccate, generally with three, but often four, mostly weak signa, sometimes with some individual variation within a species; appendix bursae is tubular or conical, posteriorly directed.

According to these diagnoses, the presence of the basal abdominal brush organ belongs to the general, plesiomorphic characters of the genus. This statement is supported by the presence of the brush organ in the closely related Himalayan–Sino-Tibetan genera *Haderonia* Staudinger, 1896, and *Tricheurois* Hampson, 1905, but also in the supposedly most ancestral Himalayan–Sino-Tibetan subgenera of *Polia*, *Protopolia* Varga, Ronkay et Ronkay, 2017, *Atropolia* Varga, Ronkay et Ronkay, 2017 and *Metallopolia* Varga, Ronkay et Ronkay, 2018 (see VARGA *et al.* 2017, 2018). This plesiomorphic organ can become lost, however, in *Polia* s. str. in several independent cases, e.g. (i) in the taxonomically rather distinct, autapomorphic lineage of *P. serratilinea* Treitschke, 1825 which possesses terminally asymmetrical saccular extensions, (ii) in the morphologically rather distinct southern Siberian species, *P. malchani* (Draudt, 1934), (iii) in three, not closely related species of the *P. nebulosa* (Hufnagel, 1766) species-group: the Central Asiatic *P. lama* (Staudinger, 1896) and the

North American species *P. nimbosa* (Guenée, 1852) and *P. imbrifera* (Guenée, 1852), furthermore (*iv*) in the closely related genus *Pachetra* Guenée, 1841.

The asymmetrisation and subdivision of the tufts of bristles on saccular extensions represent one of the most important traits of the genus (McCABE 1980). These are in plesiomorphic character stage only weakly differentiated and nearly symmetrical in certain, supposedly phylogenetically ancestral species as *P. hepatica* (Clerck, 1759), *P. subcontigua* (Eversmann, 1852), and completely reduced in *P. griseifusa* Draudt, 1950. The most differentiated asymmetrical saccular processes can be found in the polytypic species *P. serratilinea* and, obviously independently, in the Holarctic *P. nebulosa* species group (the Nearctic species are discussed in detail in McCABE (1980)). While in other species groups the tuft of bristles on the left saccular process is not (e.g. in the arcto-boreal species: *Polia richardsoni* (Curtis, 1835), *P. rogenhoferi* (Möschler, 1870) and *P. lamuta* (Herz, 1903)) or only weakly subdivided (e.g. in the *P. bombycina-purpurissata* species group), it is clearly separated into a basal and terminal tuft in the species of the *P. nebulosa* species group (McCABE 1980).

The molecular data (ZAHIRI *et al.* 2014) strongly support that the Palaearctic *P. bombycina* (Hufnagel, 1766) has two Nearctic sister species, *P. purpurissata* (Grote, 1864) and *P. nugatis* (Smith, 1898). This relation, however, was already hypothesised by McCABE (1980) in connection with the Eurasiatic origin of the whole subgenus *Polia*. Nearctic connection of the expansive Trans-Palaearctic species, *P. nebulosa* was also suggested by HEYDEMANN (1944), since *P. nimbosa* was considered by him as a subspecies of *P. nebulosa*. The Sino-Pacific *P. goliath* (Oberthür, 1880) and the Central Asiatic *P. lama* were considered as further members of the *P. nebulosa* species group (VARGA *et al.* 2019).

Biogeographically, the entire subgenus is exclusively Holarctic. However, only one single polytypic species, *P. richardsoni*, has an entire disjunct circumpolar, Holarctic distribution. Another polytypic species, *P. lamuta* has an arctic (Siberian)-alpine range. Similarly, one-one species have Nearctic sub-arctic (*P. rogenhoferi*) and boreal (*P. propodea* McCabe, 1980) distribution (McCABE 1980). Relatively few species are Trans-Palaearctic, as *P. hepatica*, *P. bombycina* and *P. nebulosa*. The taxonomically fairly isolated, polytypic *P. serratilinea* has a wide West and Central Asiatic montane steppe and European montane distribution. A set of species is connected with the montane areas of Central Asia and Southern Siberia: *P. subcontigua*, *P. malchani* (Draudt, 1934), *P. tiefi* Püngeler, 1914, *P. vesperilio* (Draudt, 1934), and *P. vesperugo* (Eversmann, 1856). These species are closely related with the relic-like West Chinese species, *P. atrax* Draudt, 1950. The Siberian montane species, occurring in the Altai-Sayan region, were allied by HEYDEMANN (1944) to the arcto-boreal species group as a “Nordgruppe” which seems to be acceptable according to their external and genital morphological features.

After these preliminary considerations, we have to answer the following questions:

- Which characters can be qualified as the most important synapomorphies (i) of the genus, and (ii) of the monophyletic species groups within the genus, respectively?
- How to distinguish these from the homoplasies?
- Which are the identical basal branches of the morphological and molecular trees?
- Which are the nodes of divergence in Holarctic species groups?
- Do they agree with the formerly established species groups of HEYDEMANN (1944) and McCABE (1980)?
- Which are the endemic vs. expansive (polycentric) species?
- Which are the monophyletic species groups and/or sister species with Trans-Beringian connections?
- What is the relative chronological sequence of these Trans-Beringian connections?

MATERIAL AND METHODS

The method of our surveys was basically classical taxonomic, but using all modern facilities from electronic databases and large collection of digitalised microscopic slides to molecular surveys (CO1 gene of mtDNA), since we worked with conserved museum material. The results of scanning electron microscopic surveys on *Polia* antennae will be published separately.

For morpho-taxonomic studies, we collected and evaluated the photographic documentation of comprehensive type materials and other important voucher specimens of *Poliina* species from several internationally valuable European collections (Berlin, Bonn, Budapest, London, Munich, Vienna, and St. Petersburg). We established the biogeographical character of all *Polia* species based on the information harboured in an electronic database of the distribution data. From all species, we prepared a series of standardised genital slides with special consideration on type specimens. As a consequence, we designated several lectotypes, recognised, and stated synonymies and composed a morphological matrix of genital characters (Appendices).

Using the genital morphological data matrices, we produced trees based on these characters (Figs 26–27 and Appendices 1 & 2). Two independent runs were allowed on data for females and males, separately, iterating for 10,000,000 generations logging every 1000. The MkV model (LEWIS 2001) for morphological data available in BEAST v2.4.7. (BOUCKAERT *et al.* 2014) was applied in all sets. Maximum clade credibility trees were created from 10,000 trees after removing 10% (50% for combined) burn-in using TreeAnnotator v2.4.7 (Bouckaert *et al.* 2014) for males only (1), for females only (2), and for males and females combined (3).

For our molecular taxonomic investigations, we collected the sequence data of all accessible *Poliina* species from published barcoding results of the North American, Central and Northern European species, and the known gene bank sequences (Fig. 28). Sequences for *cytochrome c oxidase subunit 1* (CO1) were gathered from GenBank (<http://ncbi.nlm.nih.gov/>). The average length of available DNA sequences was 649.2 base pairs,

Table 1. GenBank access numbers of analysed species.

Species	GenBank access number
<i>Atropolia (Polia) mortua</i>	JX392419
<i>Pachetra sagittigera</i>	JF415636
<i>Polia bombycina</i>	GU654989
<i>P. conspicua</i>	KT782711
<i>P. discalis</i>	KJ388193
<i>P. hepatica</i>	HQ955372
<i>P. imbrifera</i>	GU090125
<i>P. lamuta</i>	KT782486
<i>P. nebulosa</i>	HQ565374
<i>P. nimbosa</i>	GU090128
<i>P. nugatis</i>	HM868477
<i>P. piniae</i>	HM423859
<i>P. propodea</i>	GU097066
<i>P. purpurissata</i>	GU091372
<i>P. richardsoni</i>	KJ385234
<i>P. rogenhoferi</i>	HM375704

however, we used the longest sequence of all species with a length of 658 base pairs each (accession numbers listed in Table 1). This sequence length is corresponding to similar studies (e.g. HUEMER *et al.* 2014, ZAHIRI *et al.* 2014). MAFFT (KATOHI *et al.* 2005) was applied for aligning gene sequences. Then the alignments were cleaned with Gblocks (CASTRESANA 2000). The 'ape' (PARADIS *et al.* 2004) and 'seqinr' (CHARIF & LOBRY 2007) packages in R v3.4.1 (R Development Core Team 2017) were used to facilitate these steps.

A maximum likelihood approach (RAxML, STAMATAKIS 2006) was applied to find the starting tree for the Bayesian MCMC analyses conducted in BEAST v1.8.3 (DRUMMOND & RAMBAUT 2007). The best-fitted substitution model (GTR+G+I) according to the model test available in the 'phangorn' package (SCHLIEP 2011) was set, and a birth-death model of speciation was applied in the analyses (GERNHARD 2008). Two independent BEAST runs were allowed iterating for 50,000,000 generations logging every 5000. A maximum clade credibility tree was created from 20,000 trees after removing 10% burn-in using TreeAnnotator v1.8.3. (RAMBAUT &

DRUMMOND 2016). Effective samples sizes were checked in Tracer v1.7.6. (RAMBAUT *et al.* 2018), for the analyses based on morphological and also on genetic data, which allowed evaluating the initial settings for the MCMC runs.

RESULTS

Character analysis and phylogenetic interpretation

According to the genital morphology of both sexes, *Polia* (s.l.) is primarily subdivided with full support into two main branches: (i) the *nebulosa* clade vs. (ii) all other species groups. Within the latter, more heterogeneous group the monophyly of the *Pachetra*–*Metallopolia* twin clade is mostly supported which share (i) the symmetric shape of clasping apparatus and (ii) the elongate, in *Pachetra* also spiralled vesica, without diverticula and covered by extremely numerous, nearly evenly dispersed tiny spinulose cornuti (Figs 26–27). The coherence of the externally rather diverse *P. (Atropolia) mortua* (Staudinger, 1888) – *P. hepatica* – *P. griseifusa* – *P. subcontigua* complex is also strongly supported (Figs 26–27). These species are also characterised by the plesiomorphic, symmetrical character state of valvae without differentiation of sacculus

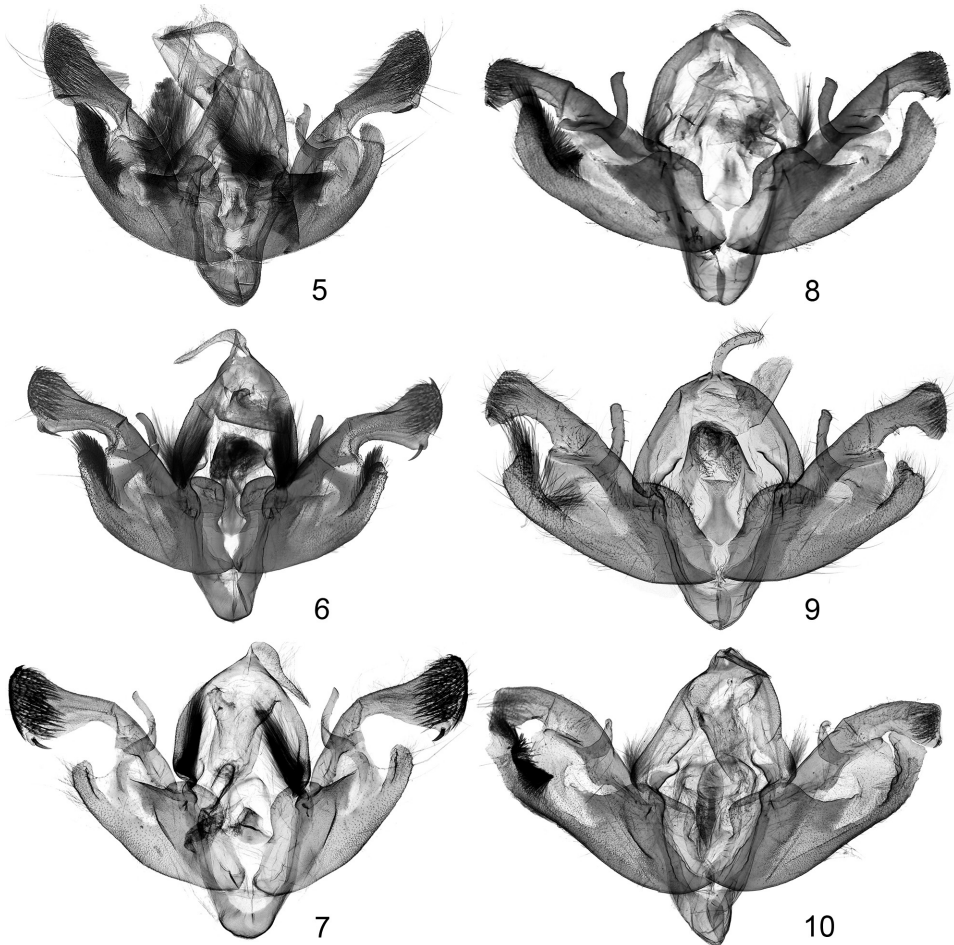
bristles, as the widespread *P. hepatica* and *P. subcontigua*, or the West Chinese endemic *P. griseifusa* with reduction of bristles. Furthermore, *P. hepatica* also shows a helicoidal configuration of the long, tubular vesica (Fig. 1), and, in female, the co-adapted sausage-shaped appendix bursae. These traits are pre-



Figs 1–4. Male aedeagus of *Polia* complex: 1 = *Polia hepatica* (Clerck, 1759), slide no. RL12391, Czech Republic, 2 = *Haderonia iomelas* (Draudt, 1950), slide no. VZ8003, China, Sichuan, 3 = *Ctenoceratoda sukharevae* (Varga, 1974), slide no. VZ9239, Mongolia, 4 = *Tricheurois cuprina* (Moore, 1881), slide no. VZ9234, Nepal

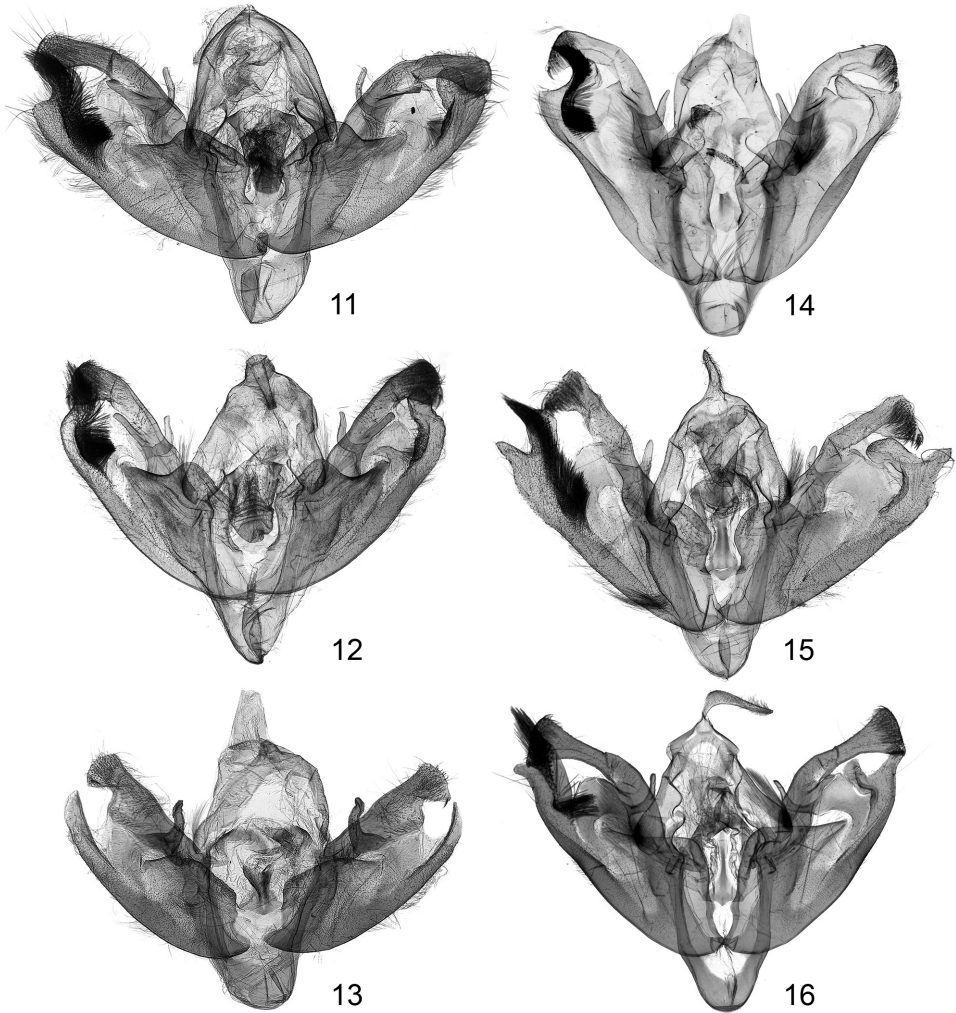
sent in somewhat similar appearance also in certain other genera of *Poliina* as *Haderonia*, *Ctenoceratoda* Varga, 1992 and *Tricheurois* (Figs 2–4) sharing also the plesiomorphic symmetrical character of the genital capsule. It is worth to note that an extreme form of the helicoidal configuration of vesica is present in the other widespread species, *P. subcontigua*, combined with the reduction of the subterminal fascia of cornuti as a unique derived character.

The saccular processes are relatively short and without well-differentiated tufts of bristles in the also otherwise distinct species *P. subcontigua*, *P.*

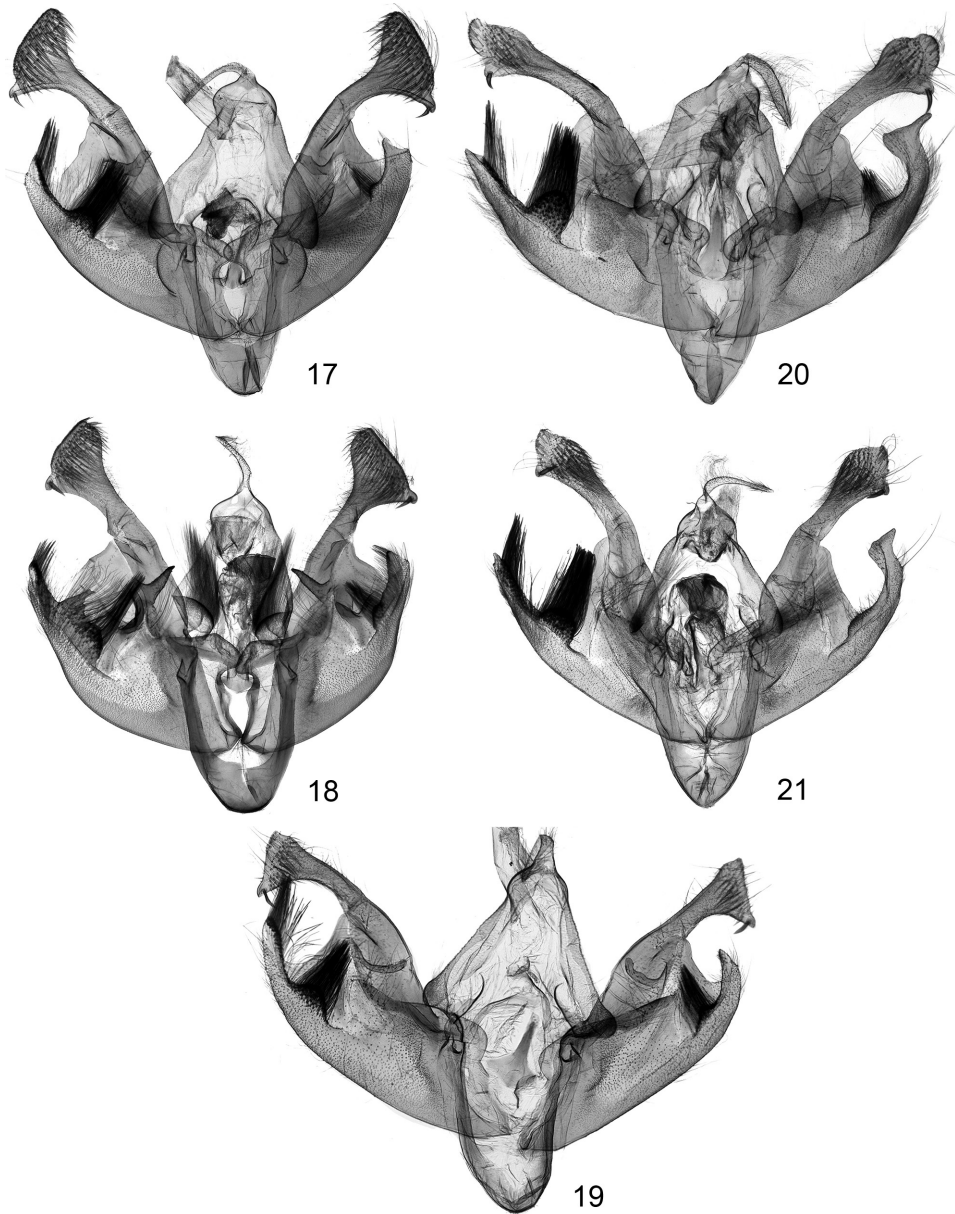


Figs 5–10. Male genital capsule of *Polia* species: 5 = *Polia subcontigua* (Eversmann, 1852), slide no. VZ9175, Kirghisia, 6 = *P. hepatica* (Clerck, 1759), slide no. RL12396, Mongolia, 7 = *P. griseifusa* (Draudt, 1950), slide no. VZ9523, China, Sichuan, 8 = *P. lamuta* (Herz, 1903), slide no. VZ8266, Sweden, 9 = *P. richardsoni* (Curtis, 1835), slide no. RL12012, Greenland, 10 = *P. rogenhoferi* (Möschler, 1870), slide no. VZ8970, North America

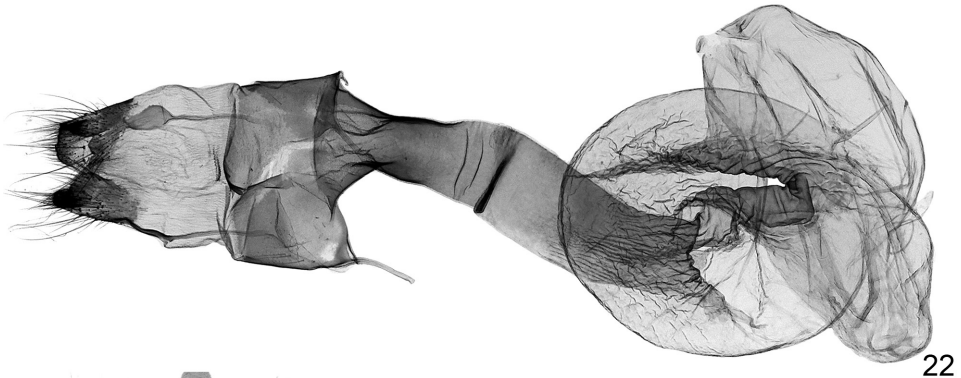
hepatica and *P. griseifusa* (Figs 5–7). In all other species, there are some obvious trends in the asymmetrisation of the genital capsule and – possibly as a trade-off – in the simplification of the vesica. The saccular processes are somewhat more elongate and are bearing a brush of stronger bristles only on the left side in the arctic-boreal species group: *P. lamuta*, *P. richardsoni* and *P. rogenhoferi*



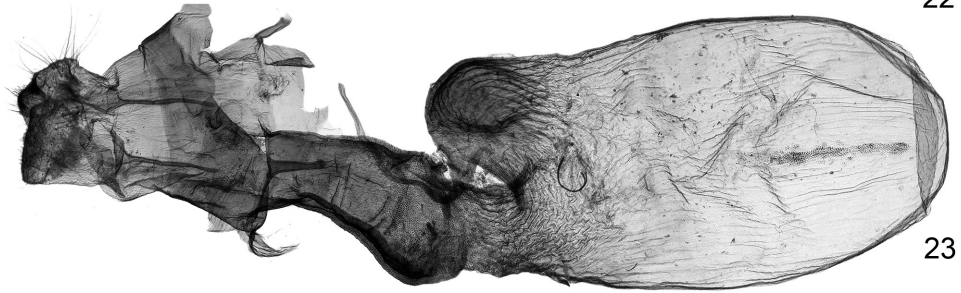
Figs 11–16. Male genital capsula of *Polia* species: 11 = *P. tiefi* Püngeler, 1914, slide no. VZ9792, Russia, Buryatia, 12 = *P. vespertilio* (Draudt, 1934), slide no. VZ9954, Mongolia, 13 = *P. malchani* (Draudt, 1934), slide no. VZ9779, Mongolia, 14 = *P. vesperugo* Eversmann, 1856, slide no. VZ2/72, Sayan Mts (holotype of *Mamestra conspicua* Bang-Haas, 1912), 15 = *P. propodea* McCabe, 1980, slide no. VZ8969, North America, 16 = *P. serratilinea* (Treitschke, 1825), slide no. KÁ1586, Greece



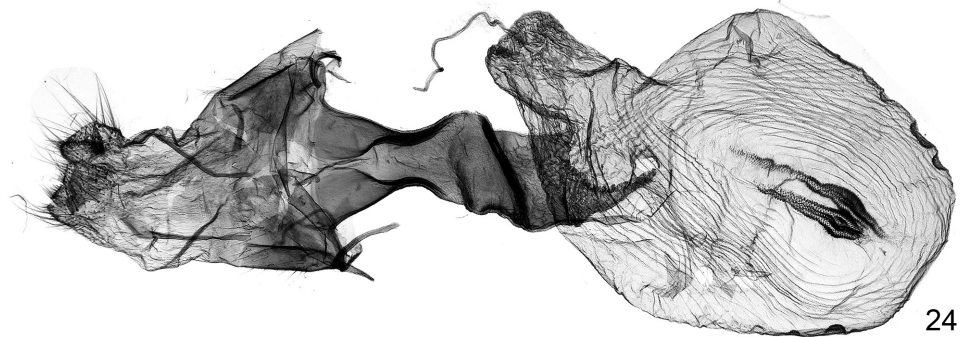
Figs 17–21. Male genital capsula of *Polia* species: 17 = *P. goliath* (Oberthür, 1880), slide no. RL11031, North Korea, 18 = *P. nebulosa* (Clerck, 1759), slide no. RL12419, Czech Republic, 19 = *P. lama* (Staudinger, 1896), slide no. VZ9783, Kirghisia, 20 = *P. discalis* (Grote, 1877), slide no. VZ8972, North America, 21 = *P. piniae* Buckett et Bauer, 1967, slide no. VZ9944, Canada



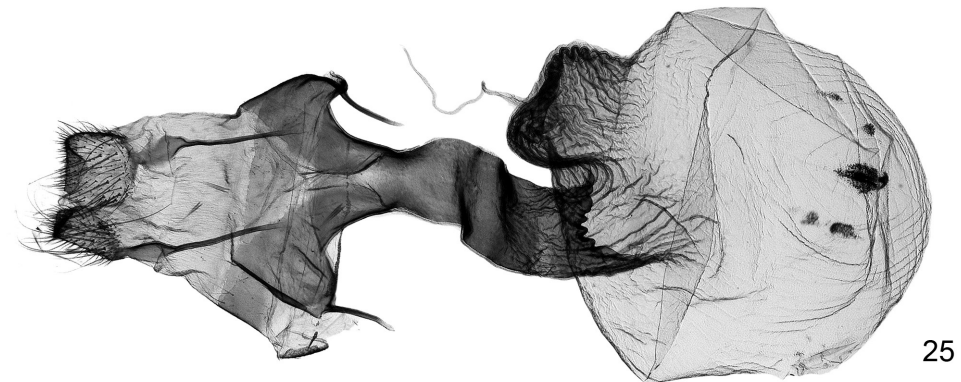
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(Figs 8–10). This “triplet” of species is also strongly supported on the genital morphological trees (Appendices 1–2). The diverse “Siberian” species group seems to be closely allied to the former species since they also have a bundle of strong bristles only on the left sacular process and the bristles on the left side are not differentiated into two tufts (Appendices, Figs 26–27). The processes are, however, more differentiated in the species of this group, i.e. these are often more or less spatulate (*P. tiefi*, *P. vespertilio*, Figs 11–12) or obtuse (*P. malchani*, Fig. 13) on the left side, and the terminal part of the right process shows a moderate trend of bifurcation (*P. vesperugo*, *P. tiefi*). This character is also present in the North American *P. propodea* which appears as a strongly supported sister species of *P. vesperugo* (Figs 14–15, Figs 26–27). The bifurcation of the terminal part of the right process is manifested in extreme form in the externally dissimilar *P. serratilinea* (Fig. 16), also characterised by a subdivision of bristles on the left process.

The former, mostly boreo-montane group is closely allied with the Holarctic *P. bombycina* “triplet” of species. The monophyly of the Trans-Palaearctic, polytypic *P. bombycina* and its Nearctic sister species-pair, *P. purpurissata* and *P. nugatis* is also strongly supported (Figs 26–27). These species show some trend of subdivision of bristles into two tufts on the left sacular process and also the appearance of some stronger bristles on the right side, mostly in *P. purpurissata*, at least in *P. nugatis*, and rather variable in different populations (subspecies?) of *P. bombycina*.

Concerning the genital structures of both sexes, the *P. nebulosa* species group proved to be the most homogenous group (Figs 26–28) in which all species show a perfect separation of bristles on the left process into a subbasal and terminal group (Figs 17–21), and the appearance of a subbasal group of bristles on the right side. The vesica is characterised in this group by the presence of a subbasal and a medial diverticulum. The distinctness of this group was already indicated by CO1 data (ZAHIRI *et al.* 2014).

Abdominal brush organ (coremata) are generally present, both in the morphologically “basal” groups as in all *Metallopolia* species but also in *P. hepatica*, *P. subcontigua*. They are also present in the species of the other groups, with some exceptions, e.g. *P. malchani* in the Siberian group, in the Eurasiatic mountain steppe *P. serratilinea*, and also in three not closely related species of the *nebulosa* species group, i.e. in the Central Asiatic *P. lama* and in the North American *P. nimbosea* and *P. imbrifera*.



Figs 22–25. Female genitalia of *Polia* species: 22 = *P. hepatica* (Clerck, 1759), slide no. RL12394, Austria, 23 = *P. vespertilio* (Draudt, 1934), slide no. VZ9972, Russia, Transbaikalia, 24 = *P. imbrifera* (Guenée, 1852), slide no. VZ9969, Canada, 25 = *P. lama* (Staudinger, 1896), slide no. RL12347, Kirghisia

The configuration of the female genitalia is rather uniform. Papillae anales are usually weakly sclerotised, rounded or obtuse, never acute. The whole antrum–ductus bursae–corpus bursae + appendix bursae apparatus is co-adapted to the elongate aedeagus and elongate tubular vesica. Ductus bursae is the shortest in the arctic-boreal species *P. richardsoni*, *P. lamuta* and *P. rogenhoferi*, and the longest, with mostly extended, funnel shaped antrum is present in the supposedly mostly derived *P. nebulosa* group (Figs 21–24). Unfortunately, in presence vs. absence of signa we could not find any phylogenetic trend since the presence vs. reduction of this trait was rather eclectic in the different species groups and in closely related species, as well. Some variations were also observed even within one single species, in accordance with the previous findings of McCABE (1980).

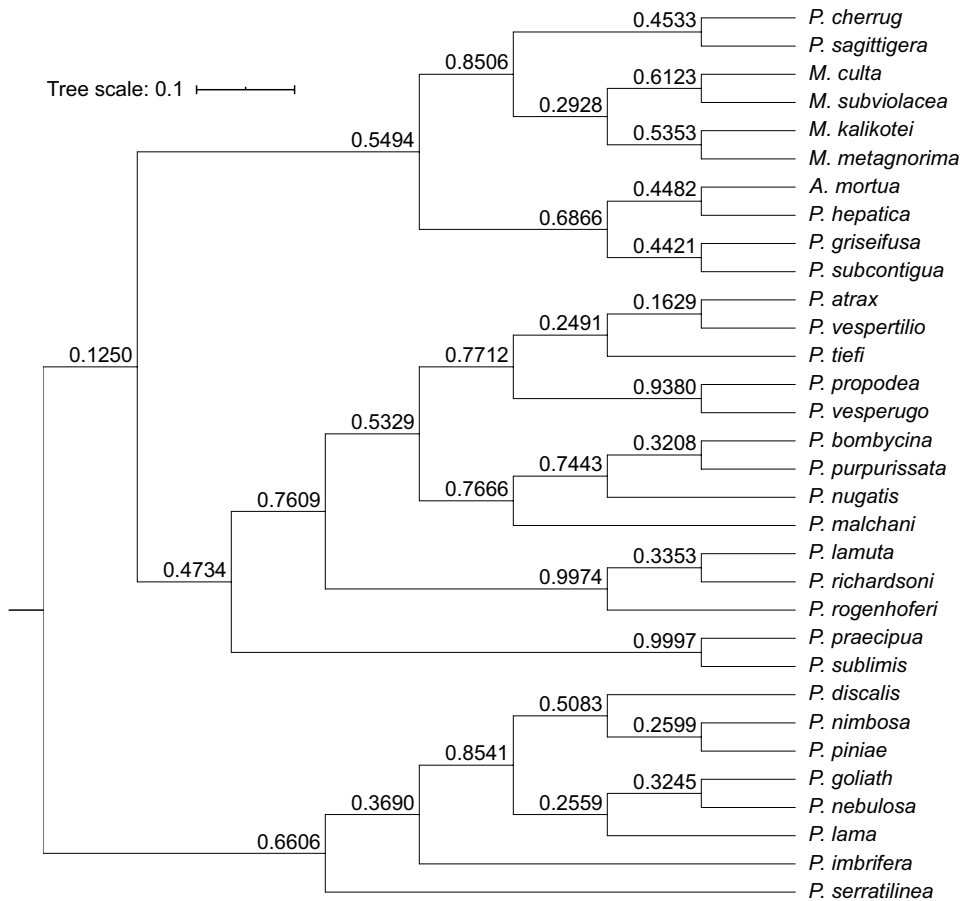


Fig. 26. Consensus tree based on discrete character data of male genitalia

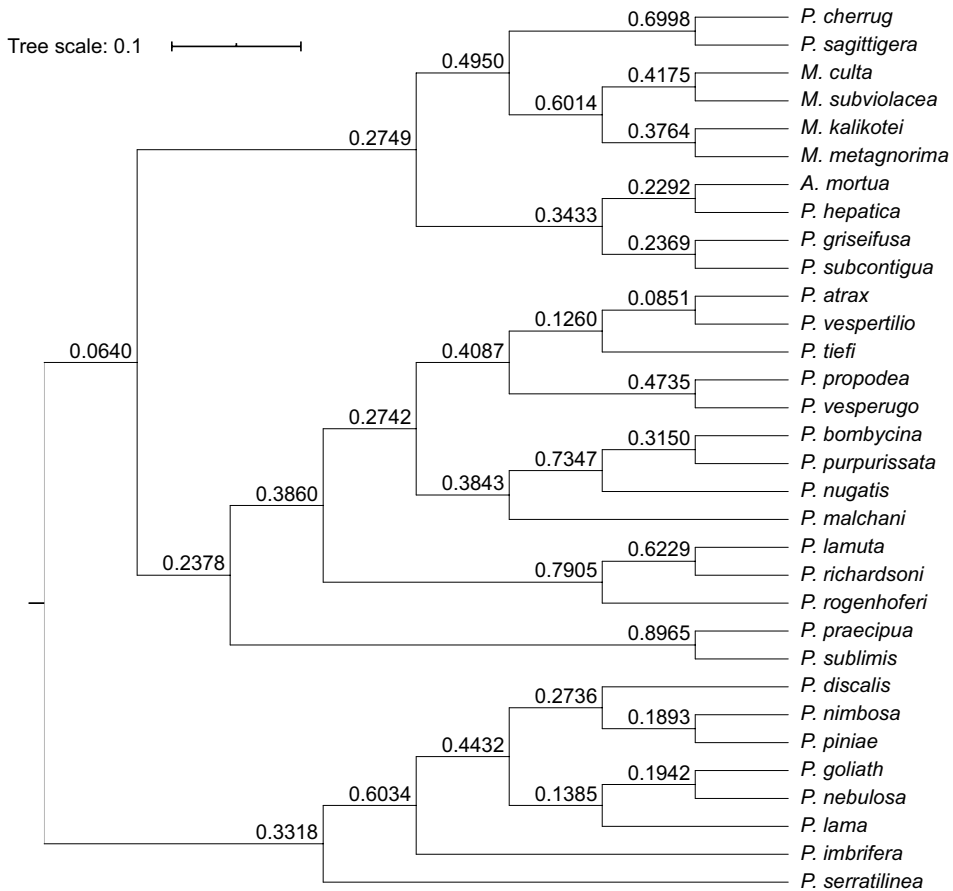


Fig. 27. Consensus tree based on discrete character data of male and female genitalia

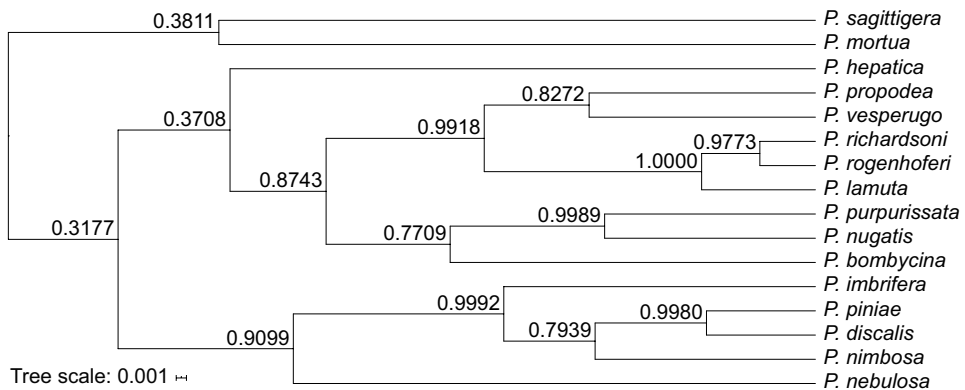


Fig. 28. Tree constructed from published barcoding results of the North American, Central and Northern European species, and the known gene bank sequences

According to our preliminary survey based on the CO1 gene our results can be summarised as follows. Since *Pachetra sagittigera* and *P. (Atropolia) mortua* appear as outgroup of *Polia* s. str., the subgenus *Polia* can be considered as a monophyletic taxonomic unit (Fig. 28). Within *Polia* the basal split was observed between the “*nebulosa* group” and all other *Polia* species, in full agreement with our morphological analysis and with the earlier traditional taxonomic and molecular works (HEYDEMANN 1944, McCABE 1980, ZAHIRI *et al.* 2014). In the *nebulosa* species group the Eurasiatic *nebulosa* species group seems to be the sister group of all Nearctic species in which *P. imbrifera* is separated from the other three species with a high support. Unfortunately, the Central Asiatic *P. lama* could not be considered failing the necessary molecular data.

In the other group of species, *P. hepatica* has shown the basal split which is plausible also according the plesiomorphic characters of the genital capsule and the helicoidal configuration of the long, tubular vesica (see also Trees 1–3). The other species are subdivided into two main groups: the mostly boreal (Siberian) and arctic species as opposed to the species triplet of the temperate Holarctic *nebulosa* species group which is also well-founded both on the morphological characters and geographical distribution of species. In this group *P. purpurissata* and *P. nugatis* are well-differentiated sister species as opposed to the widely distributed Eurasiatic *P. bombycina*. In the boreo-arctic group the species triplet (*P. lamuta* + *P. richardsoni* + *P. rogenhoferi*) is clearly separated from the *P. propodea*-*P. vesperugo* pair. However, the Siberian species which are close to the latter group (*P. tiefi*, *P. vespertilio* and *P. malchani*) remained unconsidered due to lack of the available barcode sequences.

REVISED TAXONOMICAL SUBDIVISION OF THE SUBGENUS *POLIA*

Summarising the results of the morphological characters and the preliminary molecular tree based on the barcode gene, we suggest the following taxonomic grouping of *Polia* s. str. species with some biogeographical comments.

Subgenus *Polia* Ochseneimer, 1816

Polia Ochseneimer, 1816, *Die Schmetterlinge von Europe* 4: 73. Type-species: *Phalaena nebulosa* Hufnagel, 1766, by subsequent designation by Curtis, 1829.

Taxonomically distinct Eurasiatic species without North American connections

Taxonomic notes. The following three species are not closely related to each other. They only share some similar plesiomorphic characters as the nearly symmetrical configuration of the male genital capsule with short saccular

processes, and the strong, sclerotised ampulla. Abdominal brush organ usually present. Two species are also clearly differentiated according to the sequence of the CO1 gene; furthermore *P. hepatica* shows a basal separation within *Polia* s. str. The barcode sequence of *P. griseifusa* is unfortunately unknown.

Polia (Polia) hepatica (Clerck, 1759)

Phalaena hepatica Clerck, 1759, *Icones Insectorum Rariorum cum Nominibus eorum Trivialibus, Locisque e C. Linnaei* 1: pl. 8, fig. 3. Type-locality: [?Europe] no locality given.

Taxonomic notes. This species is somewhat similar to the former one in the general shape of genital capsule but the bundle of bristles on saccular processes is slightly more expressed on both sides. The vesica has a subbasal and subterminal helicoidal torsion but with a typical, long stripe of fasciculate cornuti. The species has an extended boreo-nemoral, Trans-Palaeartic distribution with numerous colour forms but without any clear subspecific subdivision.

Polia (Polia) griseifusa Draudt, 1950

Polia griseifusa Draudt, 1950, *Mitteilungen der Münchner Entomologischen Gesellschaft* 40: 30, pl. 2, fig. 14. Type-locality: China, Prov. Yunnan, Li-kiang. Lectotype, female, in coll. ZFMK.

Taxonomic notes. This species is allied to the former one according to its external look and genital capsule. However, the bristles of the saccular processes are on both sides reduced. The configuration of the vesica is rather different, simply retroflexed dorsally with strong sclerotisation on the inner side and with a centrally positioned stripe of fasciculate cornuti. This species is known from W China (Yunnan, Sichuan) only and seems to be rather rare.

Polia (Polia) subcontigua (Eversmann, 1852)

Hadena subcontigua Eversmann, 1852, *Bulletin de la Société Impériale des Naturalistes de Moscou* 25 (1): 155. Type-locality: [Russia, Orenburgskaya obl.] "Spask.[oye]" "Jul[y]" (handwritten labels). Holotype: female, in coll. ZISP.

Taxonomic notes. This species is identical with the well-known *P. altaica* (Lederer, 1853), including the f. *monotona* (Bang-Haas, 1912); the synonymy was established by VARGA *et al.* (2017). Most populations of the species are polymorphic with variable proportion of contrastingly patterned ("typical") vs. concolorous ("*monotona*") forms without a clear geographical trend on the most part of the range with the exception of the Himalayan region where the

dark fuscous form predominate (BOURSIN 1964). The male genital capsule is nearly symmetrical with short saccular extensions but with a group of strong bristles on the left side only. Vesica is tubular, triple helicoidal, without any stripe of spinulose cornuti.

The name *subcontigua* was forgotten until the recent times, and the species was generally cited under the name *altaica*. This polymorphic species has a wide but scattered range, and is distributed from the southern Urals to Nepal on the one side and to Mongolia on the other.

Holarctic boreo-arctic-alpine group

Taxonomic notes. The following three species have essentially similar genitalia. In males, saccular processes nearly symmetrical, obtuse with a stripe of strong bristles on the left side only; ampulla strongly sclerotised, relatively thick, terminally rounded or obtuse; vesica relatively simple, up-turned dorsally, with a short stripe of fasciculate cornuti and with a small, tubercle-shaped medial diverticulum only; abdominal brush organ usually present. In females, ductus bursae relatively short, corpus bursae without signa, appendix bursae semiglobular, slightly incurved. The first two species are day-active, they have whitish hindwings with black terminal band, the third species is much larger, night-active and externally similar to the species of the next group.

Polia (Polia) lamuta (Herz, 1903)

Anarta lamuta Herz, 1903, *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg* 8: 82. Type-locality: [Russia] Uruata Camp place; W of Verkhojansk. Syntypes: 1 male, 1 female, in coll. ZISP.

Taxonomic notes. The species is subdivided to two, morphologically and geographically clearly separated subspecies. The identity of the nominotypical *lamuta* with the south Siberian alpine (Sayan Mts) ssp. *tunkinski* O. Bang-Haas, 1927 was already suggested by HEYDEMANN (1944) who considered *P. lamuta rangnowi* Püngeler, 1909 from Lapland as valid subspecies.

The ampulla is in *P. lamuta lamuta* much stronger than in *P. l. rangnowi*, terminally obtuse.

Polia (Polia) richardsoni (Curtis, 1835)

Hadena richardsoni Curtis, 1835, *Appendix to John Ross Narrative of a Second Voyage 1835*: 72, pl. A, fig. 11. Type-locality: [Canada] 15 miles from River Tatchick (Eskimo name), 200 miles S of Port Bowen, very near Comptroller's Island. Types: in coll. USNMW.

Taxonomic notes. This circumpolar Holarctic species shows intense subspeciation in both continents; the taxonomic status of the described taxa is to be clarified yet.

Polia (Polia) rogenhoferi (Möschler, 1870)

Mamestra rogenhoferi Möschler, 1870, *Entomologische Zeitung, Entomologischen Vereine zu Stettin* 31: 269. Type-locality: USA, Labrador.

Taxonomic notes. A Nearctic arcto-boreal species with a montane exclave in Colorado.

Southern Siberian–W Chinese species group

Taxonomic notes. The following species are closely allied to the former group, but they are essentially larger, mostly with dark greyish colouration and suffused markings. They have numerous specializations in the genitalia of both sexes. Saccular processes are more or less asymmetric in shape and they have a compact stripe of strong bristles on the left side only. The end of processes is more or less extended, in *P. malchani* obtuse. Vesica is relatively simple, curved with a more or less elongate stripe of fasciculate cornuti and with a medial diverticulum. Abdominal brush organ usually present, with the exception of *P. malchani* in which only the pedicel of the organ can be observed. In females, ductus bursae is tubular, mostly strongly sclerotised distally, proximally rugulose or extended, bursa with one stronger, stripe-shaped and generally with two weaker signa. The W-Chinese *P. atrax* is possibly the most ancient, relict species of this group.

Polia (Polia) propodea McCabe, 1980

Polia propodea McCabe, 1980, *New York State Museum Bulletin* No. 432: 18–19. Type-locality: Canada, Columbia, Mt. Evans, Echo Lake.

Taxonomic notes. According to the external appearance and genital configuration this species is closely related to the next, polytypic, disjunct Palaearctic species. Based on the barcode data they are possibly sister species.

Polia (Polia) vesperugo Eversmann, 1856

Polia vesperugo Eversmann, 1856, *Bulletin de la Société Impériale des Naturalistes de Moscou* 29 (3): 48, pl. 2, fig. 6. Type-locality: [Russia] Transbaikalia, Irkutsk. Lectotype: female, in coll. ZISP.

Taxonomic notes. This species was mentioned in the earlier publications as *P. conspicua* (Bang-Haas, 1912). The synonymy with *P. vesperugo* was stated and the lectotype was designated by VARGA *et al.* (2017). The geographically separated population groups of the species were originally described as distinct species (Sayan Mts: *P. conspicua* Bang-Haas, 1912; Russian Far East, Primorye distr.: *P. vasjurini* Sukhareva, 1976; North Finland, Inari: *P. sabmeana* Mikkola, 1980). They were considered as subspecies of a Siberian tundra-alpine species by HACKER *et al.* (2002), based on the presumably much larger distribution of the species (KONONENKO 1990). However, the taxonomic analysis of these externally different populations requires further studies.

Polia (Polia) tiefi Püngeler, 1914

Polia (Mamestra) tiefi Püngeler, 1914, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 28: 38, pl. 2, fig. 22. Type-locality: [Russia] Sayan Mts, Munko-Sardyk. Lectotype: male, in coll. MNB.

Taxonomic notes. This species was mentioned in the earlier publications as *P. vesperugo* (auct. nec Eversmann, HEYDEMANN 1944, HACKER *et al.* 2002) or *P. schawerdae* (Sheljuzhko, 1933). The synonymy with the latter species was established by VARGA *et al.* (2017). *P. tiefi* is widely distributed with some variation in the external appearance in the high mountains of NE Kazakhstan, South Siberia and Northern Mongolia (Saur, Tarbagatai, Sayan, Altai, Khangai and Khentij mountains), mostly in the upper mountain taiga zone.

Polia (Polia) vespertilio (Draudt, 1934)

Aplecta vespertilio Draudt, 1934, in A. Seitz, *Die Gross-Schmetterlinge der Erde* 3: 109, pl. 14, row i. Type-locality: [Russia], Irkutsk, Tunkinski Mt. Lectotype: male, in coll. MNB.

Taxonomic notes. According to the external look and the configuration of the genitalia of both sexes it can be considered as closely related to the former one. Their distribution is partly overlapping in the southern Siberian and northern Mongolian mountains; however it is more widely distributed both in West (southern Ural Mts) and East (Pacific mountains). Taxonomic interpretation of the Pacific (North Korean) population still requires further studies.

Polia (Polia) malchani (Draudt, 1934)

Aplecta malchani Draudt, 1934, in A. Seitz, *Die Gross-Schmetterlinge der Erde* 3: 108, pl. 14, row i. Type-locality: [Russia] Transbaikalia, Malchan Mt, "Borochojew", 800 m. Holotype: female, in coll. MNB.

Taxonomic notes. This is the only species of the group where the abdominal brush organ is fully reduced. It has a wide but obviously incompletely known area extending from the southern Ural Mts to the Russian Far East, Korea and Japan, seemingly without any geographical trend of variation.

Polia (Polia) atrax Draudt, 1950

Polia atrax Draudt, 1950, *Mitteilungen der Münchner Entomologischen Gesellschaft* 40: 31, pl. 2, fig. 17. Type-locality: China, Prov. Yunnan, Atuntse. Lectotype: male, in coll. ZFMK.

Taxonomic notes. The species includes two geographic subspecies, ssp. *atrax* (Yunnan) and ssp. *vargai* Gyulai et Saldaitis, 2017 (Gansu) with slight but seemingly constant differences both in external and genital characters. The bundle of bristles on the left saccular process is already slightly differentiated and the right-sided process is shorter than in other species of this group and also somewhat more obtuse.

Isolated Palaearctic steppic species

Polia (Polia) serratilinea (Treitschke, 1825)

Mamestra serratilinea Treitschke, 1825, *Die Schmetterlinge von Europa* 5 (2): 38. Type-locality: Austria, Vienna district. Lectotype: male, in coll. HNHM.

Taxonomic notes. Numerous subspecies of this externally strikingly variable species are described. The nominotypical subspecies is restricted to the eastern periphery of the Austrian Alps. Further subspecies occur in the Central and western Alps, and Alsace (*Mamestra serratilinea helvetica* Schawerda, 1925), Balkan peninsula (*Polia serratilinea kowatschevi* Drenovsky, 1931), Central Anatolia (*Polia serratilinea pinkeri* Varga, 1974), and more clearly differentiated in Central Asia (*Polia serratilinea spalax* (Alphéraky, 1887), in the Hindu-kush-Himalaya area (*Polia serratilinea tenebricosa* Hacker et Weigert, 1990), but also in western Mongolia (*Polia serratilinea eremorealis* Varga, 1974).

This species shows some convergence to *P. propodea* in the bifid terminal part of the right saccular process. The two lineages are, however, rather distant by their CO1 sequences. The asymmetrisation of the clavus and saccular processes show an evident geographical variation; its analysis and taxonomic interpretation will be treated in a further publication.

The *Polia bombycina* species-group

Taxonomic notes. The polytypical, Trans-Palaeartic *P. bombycina* is although closely related but clearly differentiated from the North American species pair *P. purpurissata* and *P. nugatis* both in morphological characters and CO1 sequences (ZAHIRI *et al.* 2014).

Polia (Polia) bombycina (Hufnagel, 1766)

Phalaena bombycina Hufnagel, 1766, *Berlinisches Magazin* 3(4): 410. Type-locality: [Germany] vic. of Berlin. Type(s) destroyed.

Taxonomic notes. The Asiatic populations of *P. bombycina* clearly show a western-eastern subdivision with some overlap in Mongolia. The west Asiatic group of populations has two contrasting forms (subspecies?) at the eastern edge of the range, (i) the dark bronze-brownish *Polia bombycina puengeleri* Lehmann, 1998, described from [Kirghisia] Alexander Mts and occurring also in Kazakhstan, and (ii) the pale fawn-coloured *Polia bombycina psammochrea* Varga, 1974, described from Mongolia, Govi Altai aimak, Khasaght Khajrhan Mts. The taxonomic subdivision of the eastern group (cf. *Polia bombycina grisea* (Butler, 1878)) described under some different names (see: VARGA *et al.* 2017) needs further surveys, as well as the populations occurring in the Caucasus range.

Polia purpurissata (Grote, 1864)

Eurois purpurissata Grote, 1864, *Entomological news, and proceedings of the Entomological Section of the Academy of Natural Sciences of Philadelphia* 9: 82, pl. 1, fig. 5. Type-locality: USA, Pennsylvania.

Taxonomic notes. The widely distributed North American species shows a considerable geographical variation. However, only *P. purpurissata apurpura* (Barnes & McDunnough, 1913) has an allopatric range (Arizona), while “*Mamestra languida* Smith, 1893” possibly represents a rare hybrid with *P. nugatis* (see: MCCABE 1980: 24).

Polia nugatis (Smith, 1898)

Mamestra nugatis Smith, 1898, *Proceedings of the Entomological Society of Philadelphia* 3: 240. Type-locality: USA, Montana.

Taxonomic notes. A species restricted to the mountainous western parts of the Nearctic in the U.S. and Canada. It has long been considered as con-

specific with the former species but is differentiated in genitalia of both sexes (McCABE 1980) and co-occurring with *P. purpurissata* in most parts of its range.

The *Polia nebulosa* species-group

Taxonomic notes. The detailed taxonomic and biogeographical survey of the species-group is recently published by VARGA *et al.* (2019). This group has a wide temperate Palaearctic (*P. nebulosa* Hufnagel, 1766; *P. lama* Staudinger, 1896; *P. goliath* Oberthür, 1880) but also Nearctic distribution (see below). The three Palaearctic species are externally forming two groups as *P. goliath* is strikingly different from the often confusingly similar *P. nebulosa* and *P. lama* though both related species have conspicuous intraspecific differentiation, too. McCABE (1980) already confirmed that four North American *Polia* species are closely related to the Eurasiatic *P. nebulosa*, and this Nearctic group of species is possibly a descendent of the “*nebulosa*”-lineage. It is differentiated from the *P. piniae* Buckett & Bauer, 1967 – *P. discalis* Grote, 1877 species-pair near to the Pacific coast, while *P. nimbosa* (Guenée, 1852) and *P. imbrifera* (Guenée, 1852) are widely distributed in the boreo-temperate zone.

Polia (Polia) nebulosa (Hufnagel, 1766)

Phalaena nebulosa Hufnagel, 1766, *Berlinisches Magazin* 3 (3): 298. Type-locality: Germany, Berlin district.

Taxonomic notes. The subspecific splitting of *P. nebulosa* is published in a separate article (VARGA *et al.* 2019).

Polia (Polia) lama (Staudinger, 1896)

Mamestra nebulosa var. *lama* Staudinger, 1896, *Deutsche Entomologische Zeitschrift, Gesellschaft Iris zu Dresden* 9: 241. Type-locality: [Mongolia, Khangay Mts] Uliassutay. Holotype: male, in coll. MNB.

Taxonomic notes. The subspecific subdivision of *P. lama* is published by VARGA *et al.* (2019).

Polia (Polia) goliath (Oberthür, 1880)

Dichonia goliath Oberthür, 1880, *Études d'Entomologie* 5: 68, pl. 6, fig. 7. Type-locality: [Russia] Askold [Island]. Holotype: male, in coll. BMNH.

Taxonomic notes. The populations occurring in Taiwan represent a distinct taxon, the description of which will be presented in a separate article.

The *Polia nimbosa*–*imbrifera* species-group

Taxonomic notes. The four Nearctic species are closely allied to the Palearctic members of the *nebulosa* group according to their external and genital morphological characters but also according to the sequences of the CO1 gene. The nearly parapatric sister species *P. discalis* and *P. piniae* occur mostly in the region of the Rocky Mountains while the other two species are widely distributed in the boreo-nemoral forest zone.

Polia discalis (Grote, 1870)

Mamestra discalis Grote, 1877, In: Uhler, *Bulletin of the U.S. Geological & Geographical Survey Territories* 3: 797. Type locality: Clear Creek Canyon (U.S., Colorado).

Taxonomic notes. *P. discalis* and *P. piniae* are sister species according to the morphological characters and also to the CO1 sequence. Abdominal coremata are present, the bundles of bristles on the left sacculus are separated, vesica with subbasal and medial diverticula. In female genitalia two signa are present only, while *P. piniae* has two stronger, stripe-like and two weaker signa.

Polia piniae Buckett & Bauer, 1967

Polia piniae Buckett & Bauer, 1967, *Journal for Research of Lepidoptera* 5: 221. Type locality: Johnsville, Plumas Co., California (Davis).

Taxonomic notes. This species and the former one are externally extremely similar. The female genitalia show the most constant differential characters.

Polia nimbosa (Guenée, 1852)

Aplecta nimbosa Guenée, 1852, *Histoire Naturelle des Insectes (Lépidoptères)* 6: 77. Type locality: "Amérique Septentrionale".

Taxonomic notes. This species shows nearly the same colour variations as *P. nebulosa* and it was considered by HEYDEMANN (1944) as subspecies of this species despite of the expressed differences in genitalia of both sexes and the reduction of the male brush organ. The most remarkable trend is in this species the rudimentation of the distal section of the left sacculus connected with the reduction of the distal bundle of bristles which also has some geographical variation. The species is widely distributed in the boreal and nemoral forest zones of North America and shows only some clinal variation with the exception of the Vancouver Island population (*P. nimbosa mysticoides* Barnes & Benjamin, 1924; see: McCABE 1980).

Polia imbrifera (Guenée, 1852)

Aplecta imbrifera Guenée, 1852, *Histoire Naturelle des Insectes (Lépidoptères)* 6: 76. Type locality: "New York".

Taxonomic notes. This species shows some simplification of the saccular processes with the reduction of the distal bundle of bristles on the left side. It means that the genital capsule secondarily seems to be more symmetrical than in other species of the *nebulosa*-group. It is widely distributed in the boreal and nemoral forest belts of North America and shows some clinal variation in colouration (McCABE 1980).

DISCUSSION

Morpho-taxonomical and phylogenetic considerations

In this survey, we focused on the sister species and species group relations within the subgenus *Polia* of the diverse and phylogenetically articulated genus *Polia*. We used a combination of the traditional genital morphological matrix and the consensus tree based on the available CO1 sequences (ZAHIRI *et al.* 2014 and GenBank, <http://ncbi.nlm.nih.gov/>).

Based on the genital morphological characters, our first statement was that *Polia* s.str., other subgenera as *Metallopolia*, *Atropolia* and *Protopolia* but also *Pachetra* together are forming a higher monophyletic unit. This result was also supported by the CO1 tree to some extent. According to CO1 data, however, *Pachetra* and *Atropolia* appear as outgroup of *Polia* s.str. which later proved to be monophyletic. Thus, our first question whether *Polia* s.str. should be considered as a monophyletic taxonomic unit was answered. Within this group, we have found a basal split between the *P. nebulosa* species group as opposed to all other species groups. Although the monophyly of the *P. nebulosa* group was fully supported, the subdivision of the other species groups was more complicated. While the basal split of *P. hepatica* was shown with rather low support, some other species groups seem to be strictly monophyletic. The most close relationship was found in the Holarctic arcto-alpine species "triplet" *P. richardsoni* – *P. rogenhoferi* – *P. lamuta*, in concordance with the published traditional morpho-taxonomic (HEYDEMANN 1944, McCABE 1980) and CO1 (ZAHIRI *et al.* 2014) results. We also could confirm the monophyly of the Holarctic-temperate *nebulosa* species group with high support, in which the polytypic trans-Palaearctic *P. bombycina* can be opposed to the Nearctic sibling pair *P. purpurissata* – *P. nugatis*.

The genital morphological trees show partly the same trends with the basic difference that the strictly monophyletic *nebulosa* species group appears to

be the counterpart of all other *Polia* subgenera and *Polia* s.str. species groups. Although we did not weight the characters, some strong derived characters of the *nebulosa*-group as the well-differentiated tufts of bristles on the left sacular process, the elongate ductus bursae with funnel-shaped antrum caused some imbalance in trees. Some former taxonomic statements were, however, strongly confirmed as (i) the taxonomic position of "*Polia*" *cherrug* as *Pachetra*, as member of the "western" phylogenetic group, sensu HEYDEMANN (1944) and (ii) the monophyly of the Sino-Himalayan *Metallopolia*. The morphological analyses also strongly supported the close relationship of the West Chinese relic species *P. atrax* with the southern Siberian mountain species *P. tiefi* and *P. vesperilio* but also with the Holarctic boreal sibling pair *P. vesperugo* – *P. propodea*. This diverse group of species is closely related both to the *P. bombycina* group, but also to the arctic-boreal "triplet" of species (*P. rogenhoferi*, *P. richardsoni*, *P. lamuta*) which already was predicted by HEYDEMANN (1944). All these species groups show the same type of asymmetry of sacular processes with a single brush of bristles on the left side, in some cases with a weak the bilateral symmetry of the male genital capsule.

The bilateral symmetry of the male genital capsule is a plesiomorphic but also a rather complex trait. It includes the symmetry vs. asymmetry of sclerotised parts, e.g. of the dilated clavus but mostly the shape of the sacular processes, on the one side, and the symmetry vs. asymmetry of bundles of bristles on the sacular processes, on the other. While the differentiation of the brushes of fixed bristles emerges typically on the left side, the dilatation or bifurcation but also the reduction of the distal part of sacular processes usually appears on the right side (see VARGA & RONKAY 2013). Both trends of asymmetry were observed in different groups of species, however, mostly expressed in the *nebulosa* species group. This group proved to be monophyletic based on the genital morphological characters of both sexes (Figs 26–27) but mostly according to the CO1 sequence (Fig. 28). This group was already predicted (McCABE 1980) and recently shown (ZAHIRI *et al.* 2014) as the sister group of all other North American *Polia*. The rather sophisticated genital capsule is often combined with some simplifications of the vesica, e.g. the loss of the fasciculate cornuti in *P. subcontigua* (combined with an autapomorphic helicoid shape of vesica), or the reduction of the medio-lateral diverticula in *P. serratilinea*. A widespread plesiomorphic character is the presence of the abdominal brush organ of males which can be reduced in several cases in not closely related species and species groups (see in detail in the results). A completely similar situation was already described in the closely related genus *Ctenoceratoda* (VARGA *et al.* 2018) but also in the phylogenetically distant *Apamea zeta*-group (Noctuidae, Apameini; see ZILLI *et al.* 2009).

Biogeographical considerations

The next step is the analysis of the biogeographical connections of the outlined phylogenetic subdivision. One of the main questions was which are the exclusively Palaearctic species and species groups, and which are those species groups in which Palaearctic-Nearctic connections can be observed. We concluded that the highest species diversity of *Polia* can be observed in the boreo-temperate zone of eastern Eurasia, and most species are typical for the montane taiga belt of southern Siberia (mostly Altai and Sayan mountain systems). Some of these species, however, as *P. subcontigua*, *P. malchani*, *P. vespertilio*, occur also in the Southern Urals. There are three species connected with arctic and/or alpine habitats. Only one polytypic species, *P. richardsoni* has a more or less disrupted Holarctic range. Its sister species *P. lamuta* also shows a long-distance disjunction, it has an arctic-subarctic range in Northern Europe (*P. lamuta rangnowi* (Püngeler, 1909)) and mountain tundra ("goltsy") occurrences from Buryatia to Yakutia (*P. lamuta lamuta*). The Nearctic *P. rogenhoferi* occurs from the Rocky Mountains to Labrador with a seemingly huge hiatus in the boreal coniferous forest zone (see: McCABE 1980). The disjunctions of these ranges are obviously results of a late-glacial, postglacial regression and fragmentation due to the expansion of the Holarctic taiga zone.

A trans-Beringian disjunction was also observed in the possible sister species pair *Polia propodea* and *P. vesperugo*. While the former species is relatively rare and recognised relatively late (described by McCABE in 1980), its Palaearctic counterpart has a huge but probably scattered range from Northern Fennoscandia to the Russian Far East and is subdivided to at least three larger population groups described as subspecies. However, the bulk of the mountain taiga faunal complex (*P. tiefi*, *P. vespertilio*, *P. malchani*) and also the mountain steppic *P. serratilinea* did not reach Beringia. It means that they could not be allied to the so-called mammoth steppe faunal assemblage. Comparing the distribution of the boreal forest and steppic, vs. the arctic-subarctic tundra species of some highly diverse genera, as *Xestia* Hübner, 1818 s.l. (including *Pachnobia* Guenée, 1852 *Anomogyna* Staudinger, 1871, *Schoeyenia* Aurivillius, 1883, *Estimata* Kozhanchikov, 1923, *Raddea* Alphéraky, 1892) or *Anarta* Ochsenheimer, 1816 s.l. (including *Coranarta* Beck, 1991, *Hadula* Staudinger, 1889, *Caloestra* Beck, 1991, *Cardiestra* Boursin, 1963, *Aglossestra* Hampson, 1905), we can conclude that the faunal complexes associated with taiga, boreo-montane forests and steppe (prairie) habitats show only scarce data of occurrence in Beringia, which refer – concerning this biogeographical group – only on a limited exchange during the Upper Pleistocene between the Nearctic and Palaearctic. In tundra habitats, in contrast, there are abundant

data on trans-Beringian faunal exchanges (LAFONTAINE & WOOD 1988, MIK-KOLA *et al.* 1991).

Two other species groups of *Polia* have Holarctic distribution and show more ancient splits. The three species of the *bombycina* species group are clearly differentiated with high support both from the former species groups and from each other, as well, and also have sizeable intraspecific variation within their fairly widely extended ranges. All these facts suggest that the ancestor of the Nearctic sister species had crossed Beringia in a relatively early temperate phase of the Upper Tertiary and consequently should have had enough time for divergence and geographical differentiation.

The CO1 dendrogram shows that the oldest Trans-Beringian wave was most probably connected with the ancestor of the Nearctic species of the *nebulosa* species group, however. We have multiple evidence for this postulate as follows:

At first: there is a considerable differentiation among and within the Eurasiatic species. *Polia goliath*, described originally as "*Dichonia*", strikingly differs externally from all other known *Polia* species. Moreover, its three major geographical population groups (*i*, Russian Far East + Japan and Korea, *ii*, Mountains of West China: Sichuan and Shaanxi, *iii*, Taiwan) are clearly differentiated, especially the actually unnamed subspecies occurring in Taiwan. Although *P. nebulosa* and *P. lama* are externally rather similar, both species have autapomorphies, like the dentate crest on the left saccular process in *P. nebulosa* or the reduction of the abdominal brush organ in *P. lama*. Furthermore, both species show mentionable intraspecific geographical differentiation (VARGA *et al.* 2019).

At second: there is a highly supported very deep split between *P. nebulosa* and all North American species despite the external similarity with some Nearctic species as *Polia discalis* (Grote, 1870) and *Polia piniae* Buckett et Bauer, 1967. These species represent an obviously monophyletic lineage.

At third: there is a considerable differentiation among the four Nearctic species, with the highest support between *P. imbrifera* and the other three species. However, all these specific splits have very probably pre-glacial origin due to the sharp differentiation of the CO1 gene. All these evidence support our hypothesis that Trans-Beringian migrations should have occurred at least three times in the zoogeographical history of *Polia*.

*

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Appendix 1. Discrete characters of *Polia* male genitalia

Species	Saccul. symm.	Saccul. length	Saccul. br. sym	Left br. subdiv	Harpe-amp.	Shape cucull.	Vesica length	Vesica coiled	Basal divertic	Medial divertic	Fascic. cornuti
<i>Pachetra sagittigera</i>	1	1	1	1	1	3	3	2	0	0	1
<i>Pachetra cherrug</i>	1	1	1	1	1	4	4	2	0	0	1
<i>Metallopolia culta</i>	1	4	2	1	1	2	3	2	0	0	1
<i>Metallopolia metagnorima</i>	1	4	2	1	1	3	4	2	0	0	1
<i>Metallopolia subviolacea</i>	1	4	1	0	1	2	3	2	0	0	1
<i>Metallopolia kalikotai</i>	1	3	2	1	1	4	4	2	0	0	1
<i>Protopolia praecipua</i>	1	1	2	1	2	1	1	1	0	1	2
<i>Protopolia sublimis</i>	1	3	2	1	2	1	1	1	0	1	2
<i>Atropolia mortua</i>	1	2	2	1	2	3	3	3	0	0	3
<i>Polia subcontigua</i>	1	2	1	1	2	3	2	4	0	0	0
<i>Polia hepatica</i>	1	1	1	1	2	3	3	3	0	1	3
<i>Polia griseifusa</i>	1	1	1	0	2	3	2	1	0	0	3
<i>Polia lamuta</i>	2	3	2	1	3	1	2	1	0	1	3
<i>Polia richardsoni</i>	2	3	2	1	3	1	2	1	0	1	3
<i>Polia rogenhoferi</i>	2	3	2	1	3	1	2	1	0	1	3
<i>Polia propodea</i>	3	3	2	2	3	1	3	1	1	1	3
<i>Polia vesperugo</i>	3	3	2	2	3	1	3	1	1	1	3
<i>Polia tiefi</i>	2	3	2	2	3	1	3	1	1	1	3
<i>Polia resperitlio</i>	2	3	2	2	3	1	3	1	1	0	3
<i>Polia malchani</i>	2	2	2	0	3	1	3	1	1	1	3
<i>Polia atrax</i>	2	3	2	3	3	1	3	1	1	1	3
<i>Polia serratilinea</i>	3	4	2	3	2	2	3	1	1	0	3

Appendix 1 (continued)

Species	Saccul. symm.	Saccul. length	Saccul. br. sym	Left br. subdiv	Harpe-amp.	Shape cucull.	Vesica length	Vesica coiled	Basal divertic	Medial divertic	Fascic. cornuti
<i>Polia bombycina</i>	2	2	2	2	3	1	3	1	0	1	3
<i>Polia purpurissata</i>	2	2	2	2	3	1	3	1	0	1	3
<i>Polia nugatis</i>	2	2	2	2	3	1	3	1	0	1	3
<i>Polia goliath</i>	3	3	3	3	2	2	3	2	0	1	3
<i>Polia nebulosa</i>	3	3	3	3	3	2	3	2	0	2	3
<i>Polia lama</i>	3	3	3	3	2	2	3	2	0	2	3
<i>Polia discalis</i>	3	2	3	3	2	1	3	2	0	2	3
<i>Polia piniae</i>	3	3	3	3	2	1	3	2	0	2	3
<i>Polia nimbose</i>	3	3	3	3	2	1	3	2	0	2	3
<i>Polia imbrifera</i>	3	2	3	3	1	2	3	2	0	2	3

Saccular symmetry: symmetrical 1, slightly asymmetrical 2, strongly asymmetrical 3

Saccular processes: short 1, medium length 2, long 3, extremely long 4

Saccular brush symmetry: symmetrical 1, slightly asymmetrical 2, strongly asymmetrical 3

Saccular brush left subdivided: 0 does not exist, 1 slightly subdivided, 2 subdivided, 3 strongly subdivided

Harpe-ampulla complex: basal plate only 1, weak ampulla 2, strong ampulla 3

Shape of cucullus: slightly extending ventrally 1, triangular 2, extended triangular 3, foot-shaped 4

Length of vesica: short 1, medium length 2, long 3, very long 4

Coiling of vesica: simply retroflexed 1, basally coiled 2, simply helicoidal 3, double helicoidal 4

Presence of basal diverticulum: no 0, one 1, double 2

Presence of medial diverticulum: no 0, one 1, double 2

Fasciculate cornuti: any cornuti 0, dispersed cornuti 1, bush of cornuti 2, fasciculate cornuti 3

Appendix 2. Discrete characters of *Polia* female genitalia.

Species	Last sternite	Last tergite	Ductus bursae	Length of ductus	Appendix bursae	Corpus bursae
<i>Pachetra sagittigera</i>	rounded 1	trapezoidal 2	str. sclerotised 2	elongate 4	tubular, rugul. 5	globular 1
<i>Pachetra cherrig</i>	rounded 1	trapezoidal 2	str. sclerotised 2	elongate 4	tubular, rugul. 5	globular 1
<i>Metallopolia culta</i>	incised 3	trapezoidal 2	mod. sclerotised 1	elongate 3	tubular, rugul 5	globular 1
<i>Metallopolia metagnorima</i>	incised3	trapezoidal 2	mod. sclerotised 1	elongate 3	tubular,rugul. 5	globular 1
<i>Metallopolia subviolacea</i>	incised3	trapezoidal 2	mod. sclerotised 1	elongate 3	tubular,rugul. 5	globular 1
<i>Metallopolia kalikotei</i>	incised3	trapezoidal 2	mod. sclerotised 1	elongate 3	tubular,rugul 5	globular 1
<i>Protopolia praecipua</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	short 1	short conic 1	elliptical 3
<i>Protopolia sublimis</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	short 1	short conic 1	elliptical 3
<i>Atropolia mortua</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	elongate 3	short conic1	elliptical 3
<i>Polia subcontigua</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	moderately long 2	tubular elong. 4	elliptical 3
<i>Polia hepatica</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	very long 4	tubular elong. 4	globular 1
<i>Polia griseifusa</i>	unknown	unknown	unknown	unknown	unknown	unknown
<i>Polia lamuta</i>	trapezoid 2	trapezoidal 2	mod. sclerotised 1	short 1	conic-oval, rug 3	glob-ellipt 2
<i>Polia richardsoni</i>	trapezoid 2	trapezoidal 2	mod. sclerotised 1	short 1	conic-oval, rug 3	glob-ellipt 2
<i>Polia rogenhoferi</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	short 1	conic-oval, rug 3	glob-ellipt 2
<i>Polia propodea</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	moderately long 2	conic-oval, rug 3	elliptical3
<i>Polia vesperugo</i>	rounded 1	trapezoidal 2	str. sclerotised 2	moderately long 2	conic-oval, rug 3	elliptical3
<i>Polia tiefi</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	moderately long 2	conic-oval, rug 3	elliptical3
<i>Polia vesperitilo</i>	rounded 1	trapezoidal 2	str.sclerotised 2	moderately long 2	conic-oval, rug 3	elliptical3

Appendix 2 (continued)

Species	Last sternite	Last tergite	Ductus bursae	Length of ductus	Appendix bursae	Corpus bursae
<i>Polia malchani</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	moderately long 2	conic-oval, rug 3	glob-ellipt 2
<i>Polia atrax</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	moderately long 2	conic-oval, rug 3	elliptical 3
<i>Polia serratilinea</i>	rounded 1	trapezoidal 2	mod. sclerotised 1	elongate 3	tubular elong. 4	glob-ellipt 2
<i>Polia bombycina</i>	rounded 1	trapezoidal 2	str. sclerotised 2	elongate 3	conic-oval, rug 3	elliptical 3
<i>Polia purpurissata</i>	rounded 1	trapezoidal 2	str. sclerotised 2	elongate 3	conic-oval, rug 3	elliptical 3
<i>Polia nugatis</i>	rounded 1	trapezoidal 2	str. sclerotised 2	elongate 3	conic-oval, rug 3	elliptical 3
<i>Polia goliath</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	globular 1	elliptical 3
<i>Polia nebulosa</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3
<i>Polia lama</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3
<i>Polia discalis</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3
<i>Polia piniae</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3
<i>Polia nimbose</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3
<i>Polia imbrifera</i>	subdivided 4	rounded 1	str. sclerotised 2	very long 4	quadratic 2	elliptical 3

